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The Vertebrate Urinary Bladder: Osmoregulatory and Other Uses

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The bladder may serve more biological uses than simple storage. The importance of bladder functions can be inferred from its presence among vertebrates, its anatomy and histology. From an evolutionary perspective, bladders have evolved at least twice in the vertebrates. The variability of permeability of the urinary bladder to water and solutes among species is discussed. Finally, the urinary bladder may play an osmoregulatory role.

The distribution of urinary bladders among the vertebrates may provide us with some clues as to their possible importance. All vertebrates do not have urinary bladders (Table 1). They appear to be present in all mammals, but with the exception of the ostrich they are absent in birds. Their presence in reptiles is sporadic: bladders are present in Chelonians and the tuatara. Some lacertilians have one, others do not. The snakes and crocodiles all appear to lack a bladder. As far as I know all the amphibians have a bladder though it can be a rather small organ, such as in *Xenopus*. The distribution of a urinary bladder is also sporadic among the fishes; some have one, many do not. Some animals that lack a bladder often utilize a surrogate organ or "fake bladder." The cloaca and large intestine appear to fulfill some bladder functions in birds and many reptiles. In some lizards such as the Australian desert species *Amphibolurus* the colon can be seen to expand considerably with stores of liquid urine [1].

Some urinary bladders can hold enormous quantities of fluid while in others it is negligible. The toad *Bufo marinus*, for instance, regularly can hold water equivalent to nearly 50 percent of its body weight in its bladder. Hirano et al. [2] compared the bladder capacities of 17 species of teleost fishes and found that this averaged only 0.5 percent of the body weight, varying from 0.3 to 0.7 percent. Some fishes, however, have larger bladders than these. Quite often terrestrial species, such as amphibians that live in deserts and which may lose water very rapidly by evaporation, have larger bladders than aquatic species [3]. For instance, a burrowing American toad, *Bufo cognatus*, has been found to hold fluid equivalent to 103 percent of its body weight in its bladder [4], while the aquatic *Xenous* can only hold less than 1 percent.

Urinary bladders appear to have evolved in vertebrates *at least* twice, which suggests that they are useful. In tetrapods the bladder is an endodermal structure which arises as an outgrowth of the cloaca. In amniotes it gives rise to the embryonic

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TABLE I
Distribution of urinary bladders among the vertebrates

Mammals	+
Birds	-
Reptiles	
Chelonia	+
Crocodilia	-
Squamata	
Ophidia	-
Lacertilia	+ or -
Rhychocephalia	+
Amphibia	+
Fishes	+ or -

\+ present - absent

allantoic membrane, part of which may persist as the bladder in the adult. While a bladder does not occur in birds the allantois remains an important organ during its development in the egg. The fish bladder is embryologically quite different to the tetrapod bladder and is mesodermal in origin, arising as an expansion of the mesonephoric ducts. It is thus really an extension of the kidney.

The structure of the urinary bladder provides some clues as to its possible functions. Its histology exhibits considerable interspecific variation. The bladder can be a highly distensible organ and as seen especially in mammals may be surrounded by a heavy muscular layer. It is lined by epithelial cells which may be one to three layers thick. These may be squamous as in amphibians, columnar as in teleosts [5], or transitional (i.e., intermediate) in mammals [6]. In teleosts the bladder appears to consist of a single layer of epithelial cells while in tetrapods there are usually three layers of epithelial cells. Different types of epithelial cells may be present but it is difficult to get precise information about this. In toads [7] there are three types, mucous cells which only make up about 1 percent of the total, cells which are very rich in mitochondria (mitochondria-rich cells) making up about 10 to 15 percent, and the more predominant granular epithelial cells the remainder. In toads these cells may have a quite formal arrangement, the granular cells being arranged hexagonally around the mitochondria-rich cells [8]. This type of pattern, however, does not appear to apply to all species, even bullfrogs. Little comparative information is available about fishes but there appears to be only one type of cell present and this is of the "mitochondrion-rich" variety [5]. It seems likely that the types of cells present and their morphological arrangement may reflect different interspecific functions that this organ may have assumed.

An organ lined with such epithelial cells not surprisingly may display a distinct permeability to water and solutes. In fact bladders show considerable variability in these permeability properties.

An active transport of Na from the urine to the blood side of the bladder has been demonstrated in most species studied, from rabbits to teleost fishes [9,10,11,12]. The tissues also display a permeability to chloride, but this normally appears to be a passive process in tetrapods but may be active in some fishes [9] and in turtles [13]. Turtle urinary bladders can also actively transport bicarbonate ions from the urine to blood [14]. Amphibian [15], and possibly turtle, bladders have been shown to acidify the urine by secreting hydrogen ions into it. Frazier and Vanatta [15] have shown that the toad bladder can also secrete NH_4^+ into the urine. Active absorption of phosphate has also been observed in the toad bladder [16].

It is difficult to make direct comparisons of the rates of active Na transport across the bladders of different species but the information which is available suggests that whether we are dealing with the rabbit, a toad, or a trout the basal levels are rather similar [17]. It may, however, change depending on conditions, such as the availability of salt to the animal. Na depletion has been shown to result in increases in Na transport from the bladders of amphibians and rabbits [18,22]. Aldosterone can be shown to stimulate this Na transport and its plasma levels appear to increase in parallel to the Na depletion so that it is no doubt contributing to the response. The extra-renal effect of this hormone is rather interesting. Aldosterone also acts on rabbit [19] and tortoise bladders [20]. It is notable that this steroid has no effect on the kidney of frogs [21] and toads [22] but it does work on their bladders so that phylogenetically it could have worked on urinary bladders even before kidneys.

The bladder of teleosts not only displays embryological and morphological differences from that of tetrapods but also physiological differences. The transmural PD across the bladder is only a few millivolts in teleosts [9,17] compared to 40 to 100 mV in amphibians, reptiles, and mammals. The electrical resistance is about 150 to 400 ohms-cm^2 in fishes [17] compared to more than 1,000 ohms-cm^2 and much higher, in the tetrapod bladder [19]. The piscine bladder is thus a "low resistance" membrane, like the gall bladder and small intestine. Teleosts don't possess aldosterone and this hormone does not appear to work on the fish bladder anyway. The control mechanism for Na transport in teleost bladder is uncertain but there is evidence that prolactin may stimulate it in some fish, in some circumstances [2,23]. Cortisol has also been implicated [23].

Urinary bladders are permeable to water. This property has been well studied in amphibians [3] and also reptiles [20,24]. In amphibians it can be strikingly increased by the neurohypophysial peptide vasotocin, a hormone which is released in response to dehydration and may mediate, or at least increase, the rate of reabsorption of bladder water under these conditions [25,26]. This mechanism does not appear to be present in other tetrapods or in fishes. The osmotic permeability of the bladders of teleosts seems to vary somewhat and appears to be low in stenohaline freshwater fishes and variable in marine fishes [2]. Euryhaline fishes may, however, change the osmotic permeability of their bladders; it is greatest in sea water and least in fresh water. Prolactin may be concerned with reducing the permeability in fresh water. However, the reports are quite variable and there may be considerable interspecific variability.

Finally I would like to consider the possible physiological use and importance of urinary bladders. This is often somewhat speculative and there may be interspecific differences in its uses. Romer [27] has said that the bladder may be "useful as a rudimentary sanitary measure." I call this the "distensible chamber pot hypothesis." Others have provided more devious interpretations and pointed out that an animal's anonymity would be severely compromised by a perpetual leak of urine, and would thus make it more obvious to predators. It may even provide a deterrent or defense mechanism which will be obvious to any one who has picked up a frightened puppy or toad. The social (and territorial) life of dogs would be rather upset by the lack of a bladder. Female turtles and elasmobranch fishes are said to utilize water stored in their bladders to wet their eggs during oviposition. Jackson [28] has shown that turtles can adjust their buoyancy by controlling the amounts of water in their bladders.

The urinary bladder may also have roles to play in osmoregulation. Charles Darwin, about 140 years ago, in his account of the voyage of H.M.S. *Beagle* [29] described the apparent use of water stored in the bladders of frogs and tortoises to maintain their hydration (and also that of the humans that hunted them!). "I believe it is well ascertained, that the bladder of the frog acts as a reservoir for the moisture necessary to its existence: such seems to be the case with the tortoise. For some time after a visit to the springs, their urinary bladders are distended with fluid, which is said gradually to decrease in volume, and to become less pure. The inhabitants, when walking in the lower district, and overcome with thirst, often take advantage of this circumstance, and drink the contents of the bladder if full; in one I saw killed, the fluid was quite limpid, and had only a very slightly bitter taste" (Charles Darwin, 1839).

Urine stored in the bladders of amphibians [26] and chelonians [30] has been observed to become more concentrated and may be reduced in volume when the animals are dehydrated. It appears that these stores of urine may be useful when such animals are foraging for food, especially under dry conditions [31]. Desert-dwelling amphibians may seek refuge in burrows and estivate for many months when rain does not fall. Under such conditions the stores of water in the bladder appear to provide a useful buffer, especially to act as a "sink" where solutes such as urea may be sequestered.

We have far less information about the potential physiological significance of salt reabsorption from the bladder. Two possible functions have been considered: *i.* further reabsorption of urinary electrolytes may occur, and/or *ii.* the maintenance of the concentration gradients established by the kidney may be facilitated. Bladder urine concentration has often been observed to be lower than that of ureteral urine in amphibians. It seems likely that salt reabsorption could be useful, especially in species that live in fresh water and which may be subjected to a salt deficiency. This could also apply to fresh water fishes. In teleosts salt uptake could in addition be useful in sea water as the reabsorption of salt and accompanying water from the bladder could reduce the necessity to drink sea water. Howe and Gutknecht [32] are, as far as I am aware, the only ones that have made a proper quantitative assessment of this effect. In toadfish (*Opsanus tau*) they have found that in the absence of salt and water absorption from the bladder such fish would have to drink 10 percent more sea water. The physiological and adaptive significance of this effect is difficult to assess.

The mammalian urinary bladder would appear to have a unique osmotic function as this group of vertebrates is the only one possessing a bladder which can form a hyperosmotic urine [33]. In contrast to other vertebrates, it must therefore be able to withstand and maintain what are often considerable osmotic gradients and high concentrations on its mucosal surface. These concentrations would be sufficient to considerably modify the permeability of the amphibian bladder. The mammalian bladder must be rather special and one suspects that its permeability to water must be very low, but I can find no acceptable measurements of this. Lewis and Diamond [19] have considered the aldosterone-sensitive transepithelial Na transport which they observed *in vitro* in the rabbit bladder. Based on their observations they estimated that during an overnight period only about 13 percent of the Na in the urine would be reabsorbed. Not a very impressive performance, but who knows what the picture is in a severely Na-depleted animal. The ion-transporting activity may however be necessary primarily as a conservation measure to maintain the concentration gradients established by the kidney.

Urinary bladders may, it appears, have diverse uses and salt and water transport and osmoregulation may only be one and probably is not even the most important of these.

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